FEEDING HABITS OF THE SAND SHRIMP
CRANGON SEPTEMSPINOSA[1]

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The sand shrimp *Crangon septemspinosa* Say is a common estuarine decapod distributed along the northwestern Atlantic from Newfoundland to eastern Florida (Squires, 1965; Williams, 1955, 1965; Price, 1962). Although *C. septemspinosa* is carnivorous (Price, 1962; Regnault, 1970), it also may ingest organic matter in various forms.

Crangon spp. has diverse feeding habits. Lloyd and Yonge (1947) classified *Crangon vulgaris* (= *Crangon crangon*), an European species, as an omnivore after finding algae, polychaetes, gastropods, bivalves, amphipods, fish eggs and fish larvae in the digestive tract. However, they felt that *C. vulgaris* preferred animal tissues. Allen (1960) categorized *Crangon allmani*, another European species, as a carnivore, but noted that sand and mud particles were always found in the stomach. Tiews (1968), in reviewing the literature on *C. crangon*, considered that the species was an omnivore, but animal tissues did comprise the main food items. Kosaka (1970) classified a Japanese species *Crangon affinis* as a carnivore, but sand and mud were always present with the food.

Williams (1955, 1958) found a variety of recognizable and unrecognizable material in the alimentary canal of three species of penaeid shrimp and believed that "softer and more easily digested materials could easily form the bulk of the diet" [1955, page 143]. Dahl (1968) noted that the food of several Australian prawns was small animals and a large amount of unrecognizable material, which might form the main component of the diet. To derive this material, shrimp browse on the microorganisms (bacteria, algae, and microfauna), which grow on the substratum. Frankenberg and Smith (1967) found seven crustaceans that ate fecal material. Also Johannes and Satomi (1966) observed that the grass shrimp *Palaemonetes pugio* assimilated the organic material in and on fecal pellets.

An ability to utilize diverse foods has survival value in a seasonally changing environment. Thus, when preferred food is scarce, organic debris is usually available to estuarine animals (Darnell, 1967, 1968; Odum and de la Cruz, 1967; Odum, 1971).

The objective of this study was to determine the kinds of food utilized by *C. septemspinosa*. Stomach contents and time of feeding were observed in a natural population; rate of digestion and growth performance on prepared diets were evaluated in the laboratory.

Materials and Methods

Collecting area

Shrimp were seined (2 × 1 m; 2 mm mesh) from sand flats in the Pettaquams-cutt River, Rhode Island, near Sprague Bridge (41° 26′ 55″ N, 71° 27′ 05″ W). This river empties into Rhode Island Sound near the mouth of Narragansett Bay. The station had the following characteristics: water depths of 0.5–1.0 m, average salinity of 27‰, fine to coarse sand, and current velocities of approximately 20–30 cm/sec at full tidal flow.

Stomach analyses

From May to October, 1971, a total of 225 stomachs were examined. Shrimp were collected during the day; those selected had the anterior chamber of the proventriculus expanded with material, which could be seen through the carapace. The shrimp were frozen immediately; after thawing the carapace was lifted and the internal organs exposed. The stomach was removed and opened on a microscope slide. The contents were examined with a dissecting microscope (9–75 ×) and identified. Frequency of occurrence was expressed as the number of stomachs in which each food item occurred as a percentage of the total number of individuals examined. Volumetric importance of each food type was made by visual estimate.

Time of feeding

Sampling was conducted over a 24-hour period on July 7 and 8, 1971. Each hour, 30 shrimp were selected randomly from seining and frozen immediately. Later estimates of stomach fullness were made (full, half-full, and empty). The contents of full and half-full stomachs were examined for trituration.

Rate of digestion studies

Shrimp, 15 to 54 mm in length, were collected on July 20, 1971 and were separated into 5 mm size groups. Three shrimp from each group were placed in a plastic container (20 × 20 × 40 cm) with holes drilled in the sides for water circulation. The vessels, which contained 1–2 cm of clean sand, were covered and submerged in a water table (15 cm water depth).

Seawater was filtered through a sand bed (30 × 50 × 30 cm) to remove particulate material before flowing through the water table. The filter retained approximately 93% of the chlorophyll *a* in the entering water (chlorophyll determined by a method of Strickland and Parsons, 1965). The flow rate through each filter was approximately 550 ml/min. Each water table had two filters.

Three diets of varying texture were tried: tissues of *Crangon*, fish meal (Point Judith Fisherman's Cooperative, Point Judith, Rhode Island), and the clam *Mercenaria mercenaria*. All tissues were dehydrated, and 6 g of each diet were mixed with 0.5 g of carmine and 30 ml of 2.2% agar (Bacto-agar, Difco Laboratories, Detroit, Michigan).

Before each trial, shrimp were starved for two days. Blocks of food were then placed in each compartment; and upon ingestion, the dyed food was easily seen

through the carapace. During the first 6 hours, the shrimp were observed hourly for reduction of coloration in the stomach and for its appearance in the intestine. One shrimp from each of the three feeding groups was sacrificed each hour over the 6-hour observational period, and estimates of the rate and degree of physical digestion of its stomach contents were made. Inspections were also made at 12 and 24 hours after feeding.

Feeding studies

All procedures were as described previously, except that the experiments were 8-weeks long. Growth was estimated from successive measurements (to the nearest mm) on the same individual every 2 weeks.

The following diets were tested: *Candida sake,* a marine yeast isolated from macrovegetation taken from tide pools at Narragansett, Rhode Island and grown in malt extract broth (25 g/l of seawater) ; Baker's yeast (Fleishmann's Yeast, Standard Brands, Inc., New York) ; brine shrimp (Metaframe Co., San Francisco, California) ; an unknown bacterium, probably a member of the *Pseudomonas* group isolated from Narragansett Bay seawater and grown in an "OZR" medium (1.0 g yeast extract and 1.0 g trypticase/l of seawater) ; calanoid copepods taken over a year's period in Narragansett Bay ; *Spartina alteriflora* detritus and attached microflora collected at Bissels Cove in North Kingston, Rhode Island (the size fraction between 0.500 and 0.017 mm) ; TetraMin, a tropical fish food (TetraKrafteWerke, West Germany) ; finely chopped hard-boiled egg ; and glycogen obtained from Nutritional Biochemical Co., Cleveland, Ohio. All other foods were as described previously.

Foods were dehydrated by heat or freeze-drying. Six gram portions were mixed with 30 ml of 2.2% agar ; the gel was cut into 2 g blocks, which were fed to the shrimp daily.

Experiments were run during spring, summer, late summer, and fall ; mean water temperatures were 15, 20, 20, and 17° C respectively. Controls were given fresh clam tissue. A second control was maintained without food during the summer and late summer experiments.

The growth rates were calculated according to the following equation which permits comparisons among groups of growth curves but makes no assumptions about the growth model (Rao, 1958) :

$$B = \sum g_i \; X_i$$

where B = growth rate in arbitary units; g_i = the sum of the growth increments in mm among all treatments for each growth period; X_i = the size increment for each shrimp during each growth period; and i = the number of incremental periods. To equalize the variances, the growth rates were transformed by square root.

Treatments within each season were compared by one-way analysis of variance (Ostle, 1963). Fisher's Least Significant Difference (LSD) was used for pairwise comparison of groups with multiple means (Fryer, 1966). If two means differed by the LSD calculated at a preselected probability, they were statistically different.
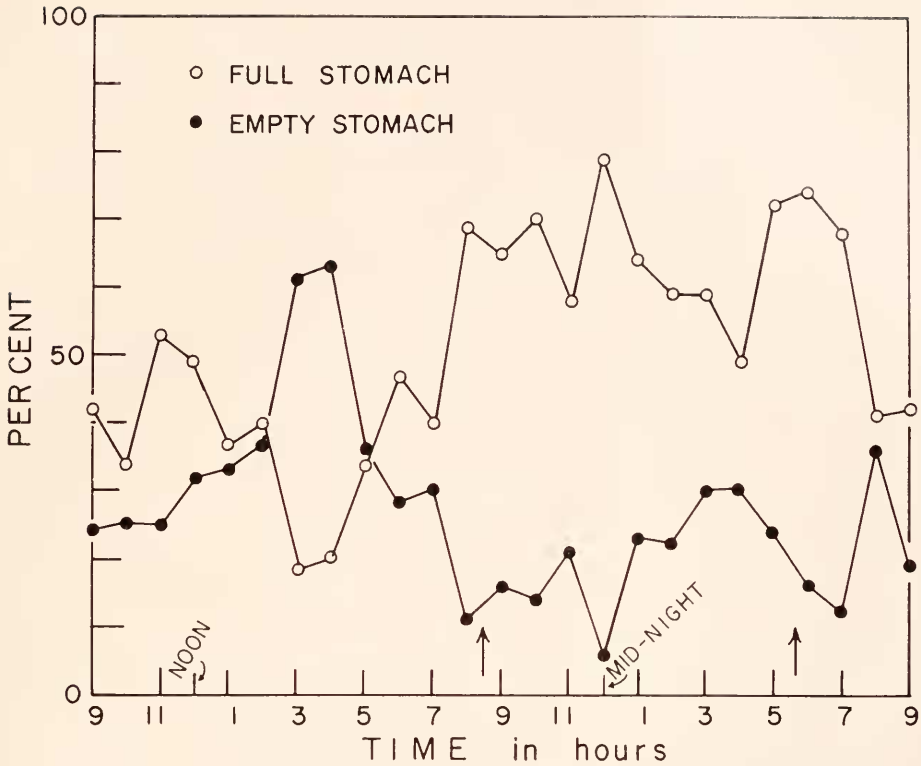
FIGURE 1. Stomach fullness compared with time of day for a field population of *C. septemspinosa*. The arrows indicate the time of sunset and sunrise.

RESULTS

Stomach analyses

In terms of volume and frequency of occurrence, organic debris, sand, and crustacean parts were the major components of 225 stomachs examined. Organic debris comprised 85% of the volume and occurred in all the stomachs examined. Sand had a frequency of occurrence of 76% and comprised approximately 4% of the total volume. Crustaceans parts occurred in 57% of the stomachs examined and accounted for 8% of the total volume. Minor food items (< 1% frequency of occurrence) included: copepods, plant material, polychaete fragments, amphipods, mollusks, fecal pellets, fish scales, nematodes, ostracods, and eggs from invertebrates. Seasonal trends in the proportions of dietary components were not apparent.

Time of feeding

Based on stomach fullness, the major feeding period was at night (Fig. 1). The onset of feeding seemed to be initiated at darkness (sunset on July 7 was 8:32 DST), and feeding activity peaked once at midnight and again approximately at dawn (sunrise on July 8 was 5:40 DST).

TABLE I

Mean growth rates ($\bar{x} \pm sd$) of C. septemspinosa fed the respective diets during four seasons. The growth rates, B, may be compared within seasons, but should not be compared between seasons because of data transformations. Note the mean water temperature for each season. All dried foods were embedded in an agar binder. See the text for the source and preparation of the foods and for an explanation of Categories I–IV. Fisher's LSD was calculated at $P = 0.05$; $N = 12$ for each determination except fall, where $N = 23$.

Food	Spring 15° C	Growth rate B		Fall 17° C
		Summer 20° C	Late Summer 20° C	
Category I				
Fresh *Mercenaria*	14.18 ± 3.31	13.02 ± 3.54	21.38 ± 5.17	
Frozen *Artemia*			21.95 ± 4.31	30.48 ± 5.63
Hard-boiled egg				28.34 ± 5.37
Category II				
Dried fish meal	10.94 ± 2.47			28.34 ± 6.01
Freeze-dried *Crangon*	10.87 ± 3.19		17.82 ± 6.97	
Freeze-dried *Mercenaria*	10.06 ± 1.93			
Freeze-dried copepods		8.76 ± 2.05		
Freeze-dried *Artemia*			15.06 ± 4.14	26.01 ± 3.20
Category III				
Freeze-dried beef liver	9.37 ± 2.94			
Freeze-dried marine yeast	9.24 ± 2.68			
Agar + glycogen (0.5 g)	8.92 ± 2.43			
TetraMin (dried)		7.09 ± 1.96		
Baker's yeast (dried)		7.65 ± 2.80		
Freeze-dried *Spartina* detritus		6.42 ± 1.49		
Freeze-dried bacteria			9.77 ± 2.91	
Frozen bacteria				20.74 ± 3.73
Category IV				
Starved	4.61 ± 4.23	2.83 ± 3.01	5.40 ± 5.21	7.68 ± 6.67
LSD	2.42	2.11	4.06	3.05

Shrimp with full or half-full stomachs were examined to estimate the degree of trituration. Food retained its identity for approximately 2 hours after sunset.

Underwater observations in nature showed that *C. septemspinosa* fed on fresh animal tissue. During the day, *Crangon* were immediately attracted to shucked mussel (*Mytilus edulis*) and would ingest the tissue within two minutes.

Rate of digestion studies

A few minutes after the ingestion of dyed food, the cardiac stomach and hepatopancreas became bright red. Within an hour of ingestion, food and dye reached the intestine, and production of fecal pellets began shortly thereafter. Coloration faded over time, and by 6 hours the hepatopancreas was pale pink. The color did not diminish further because the dye was apparently incorporated into the tissue of the digestive diverticula.

Stomach contents were examined 1 hour after feeding. Paste-like consistency indicated efficient trituration by the gastric mill. The cardiac portion of the stomach was empty 6–12 hours after feeding.

Feeding studies

Comparisons within seasons (Table I) showed the growth rates differed (analysis of variance, $P = 0.01$; Fisher's LSD, $P = 0.05$) between treatment means. Because of data transformations, mean growth rates should not be compared between seasons.

Foods may be classified into four categories based on origin and processing: Category I—fresh or frozen animal tissues generally of marine origin (*Mercenaria, Artemia,* and hard-boiled egg); Category II—dried animal tissues of marine origin (*Crangon,* fish meal, *Mercenaria,* copepods, and *Artemia*); Category III—dried animal and microbial tissues (beef liver, marine yeast, agar, TetraMin, Baker's yeast, *Spartina* detritus, bacteria); Category IV—starved. To rule out seasonal influences, the growth increments within each of the four categories were pooled and new growth rates were calculated. Within each category, most treatments were found to produce equal growth rates (analysis of variance; $P = 0.05$). Mortalities for the 8-week period were: Category I—10%; Category II—30%; Category III—40%; Category IV—55%.

Starved groups were used for only the summer and late summer groups, but the results were extrapolated to spring and fall. An assumption of this extrapolation was that metabolism of starved shrimp would be maximal when the water temperature was the warmest (the summer months) and that the rates would be lower at cooler water temperatures.

Since there were always significant differences in growth rates between the starved groups (Category IV) and the others, *C. septemspinosa* derived some nutritional value from all the foods that were offered. The shrimp grew best when eating fresh animal tissues generally of marine origin (Category I), but to a lesser extent, they utilized and grew on other organic material.

DISCUSSION

Organic debris was a major component in the field diet of *C. septemspinosa.* It had several origins because detritus as well as tissues made undistinguishable by trituration were included in this category. Sand in the diet probably contributed adsorbed organic compounds and associated bacteria, which could serve as nutrients (Odum, 1971), but sand could also assist in trituration (Tiews, 1968).

Since the data for stomach analyses were taken during the daylight hours and the shrimp generally fed at night, it was possible that trituration made identification of food items difficult. The shrimp might have ingested anything of caloric value that was encountered, but it would be rapidly and efficiently reduced to organic debris.

Based on results similar to our data, Price (1962) classified *C. septemspinosa* as a secondary consumer. He found that organic debris comprised approximately 60% of the material ingested; each of nine other groups contributed less than 10%. Various sources of crustaceans (involving five groups) accounted for 24% of the volume. Our data showed that crustaceans (crustacean parts and copepods)

comprised only 9% of the volume. The difference might be due to the uncertainty of estimating volumes or the difference may be attributed to crustacean abundances between Delaware and Rhode Island. Price (1962) also noted variations in the stomach contents over a 7-month period. Such variation may have arisen from availability and not preference for specific foods.

Crangon septemspinosa, C. crangon, C. allmani, and *C. affinis* are carnivores (Lloyd and Yonge, 1947; Allen, 1960; Price, 1962; Tiews, 1968; Kosaka, 1970; Regnault, 1970). However, a wide variety of materials found in the digestive tracts (*e.g.,* mud, sand, algae, detritus) suggests that *Crangon* spp. ingest anything encountered. The identity of many items is quickly destroyed by trituration. The resistance of chitin, shells, and setae to digestion and slow passage of these items through the digestive tract may bias the results towards carnivoristic feeding. The large amount of unidentifiable organic detritus found by Price (1962) and our study suggest that detritus is a dietary constituent.

Much of the organic debris noted in the stomachs of the shrimp may be of plant origin. Generally this cellulose is of limited nutritional or caloric value because of degradation by bacterial and leaching processes (Nykvist, 1959; Darnell, 1967; Odum and de la Cruz, 1967; Kormondy, 1968; Udell, Zanudsky, and Dohery, 1969). The nutritional value of this detrital material is derived from the extensive microflora (protozoa, bacteria, yeast) that colonizes the surface (Russell-Hunter, 1970; Odum, 1971).

Organic matter may also be derived from the aufwuchs community that develops on macrovegetation (Brown, 1962). Appendages and mouth parts of the shrimp are modified for collecting and ingesting small particles such as benthic diatoms. Diatom frustules and aufwuchs were not found in the stomachs of *C. septemspinosa,* so the ecological significance of this material is uncertain.

The anterior chamber of the proventriculus of *Crangon* acts as a crop for food that is cut and masticated by the mandibles or for food that is small enough to be gulped (Dahl, 1968; Tiews, 1968). The gastric mill reduces the food to a paste where it then passes into the digestive diverticula of the hepatopancreas for digestion or onto the mid-gut for osmotic regulation and defecation. Dahl (1968) noted similar rates for ingestion, passage of food to the hepatopancreas, and defecation as we observed with *C. septemspinosa.*

The incorporation of the carmine ($< 5\ \mu$ diameter) into the tissues of the hepatopancreas was in direct contrast to the work of Forster and Gabbott (1971). They noticed no uptake of chromic oxide by the digestive diverticula of the prawns *Palaemon serratus* and *Pandalus platyceros.* The efficient action of the pyloric filter in the prawns apparently prevented the chromic oxide from passing into the diverticula of the hepatopancreas. In contrast, *Crangon* does have a gastric mill and presumably does not need as an efficient pyloric filter, which would permit some of the carmine to enter and stain the hepatopancreas.

Our data show that a variety of foods are of nutritive value to *C. septemspinosa.* Foods that promoted the best growth in the laboratory (Category I) are the preferred foods in nature. However, results demonstrate that representative microflora associated with *Spartina* detritus supply nutrients to *C. septemspinosa.*

Forster and Gabbott (1971) showed that prawns assimilate foodstuff of animal and vegetable origins. Bärlocher and Kendrick (1973) found that the amphipod *Gammarus pseudolimnaeus* utilizes the fungal populations on leaf litter. Sick,

Andrews, and White (1972) demonstrated that semipurified diets provide nutrients to penaeid shrimp much better than natural foods. Decapods have a full complement of digestive enzymes (*i.e.,* proteases, lipases, and carbohydrases; Yonge, 1924; Vonk, 1960; Dahl, 1968) allowing the organism to digest and utilize the bulk of the material ingested. Therefore, the limitation of feeding may not be due to digestibility, but with supplying the proper nutrients (*i.e.,* having a small C : N ratio; Russell-Hunter, 1970) and with the olfactory stimuli to find and ingest the food (Barber, 1961).

Olfactory quality could account for the different rates of growth between food Categories I, II, and III (Table I). Drying, either by heat or freeze-drying, apparently removed enough of the chemical stimuli to reduce the olfactory quality (see Wilcox, 1972). The difference was most obvious between foods of Category I and II, where the difference in growth may be attributed to drying.

The reduced growth rates in Category II and III had two possible causes: olfaction and nutrition. Foods of non-marine origin (*e.g.,* Baker's yeast) could be lacking the olfactory chemicals that evoked feeding responses. Also these foods could be lacking or low in essential amino acids, lipids, or other nutrients required by the shrimp. For example, frozen bacteria were avidly consumed, whereas the freeze-dried bacteria was ingested to a lesser extent; the difference was probably due to olfactory stimuli. For the freeze-dried and frozen bacteria, no difference was observed in the growth rates (Table I, Category III), which seemed to indicate that the shrimp were not receiving a nutritionally balanced food. In contrast, when hard-boiled egg was fed to the shrimp, growth was equal to that realized by shrimp fed foods of marine origin.

Observations on the behavior of *C. septemspinosa* show that it follows a zig-zag path as the shrimp homes on the scent of food (Wilcox, 1972). Similar types of homing behavior are also common for other crustaceans (Pardi and Papi, 1961). The chemical stimulus for feeding appears to be general, because non-marine substances (*e.g.,* Baker's yeast, hard-boiled egg) evoke the response (Wilcox, 1972). Foods that are preserved by drying, however, are often not ingested. Heat or freeze-drying apparently modifies or removes water-soluble compounds that are presumably responsible for initiating the feeding response. The unsuitability of dried foods, then, is not necessarily in the nutritional quality of the food, but in the ability of the shrimp to locate it. Interesting areas for future research are the separation and understanding of olfactory and nutritional qualities of food.

For a complete feeding cycle, an organism must be stimulated by olfaction to seek the food, the food must satisfy the taste and tactile receptors, and, finally, feeding stops when the stomach is full. At any stage the organism may reject a food item. Preferences may exist, and the animal may seek these foods first, but if these preferred components are scarce in the ecosystem and the animal is hungry, it will ingest a variety of substances until satisfied. The term omnivore is aptly applied to *C. septemspinosa*.

Nutritional requirements of arthropods are known to be specific (Provasoli, Shiraishi, and Lance, 1959; Provasoli and Shiraishi, 1959; Provasoli and D'Agostino, 1962, 1969; Takano, 1967; Subrahmanyam and Oppenheimer, 1969). Poor growth in several of our experiments may be due to nutritional deficiencies of the

food. Regnault (1970) has demonstrated the importance of a proper diet for optimum growth of juvenile *C. septemspinosa.*

Welsh (1970) determined that *C. septemspinosa* was active at night. Hagerman (1970) found that the locomotory activity of *C. vulgaris* began at darkness and observed 2–3 periods of peak activity during 16 hours of darkness. These results agreed with 2 periods of nighttime feeding activity we observed (Fig. 1). Our data also indicate that *C. septemspinosa* is an opportunistic feeder. They feed predominantly at night, but they will take preferred foods during daylight hours.

Haefner (1969a, 1969b, 1970, 1971, 1972) and Huddart and Arthur (1971) showed how *Crangon* spp. respond and adapt to physical and chemical variations encountered in an estuary. Unspecialized feeding is also believed to be another adaptation by *C. septemspinosa* to cope with the vagaries of food in the estuary.

SUMMARY

Laboratory studies were conducted to compare growth rates of the estuarine sand shrimp *Crangon septemspinosa* on various natural and artificial diets. Field studies examined the types of food consumed by the shrimp.

In nature, 85% of the material in the stomach is organic debris; sand, crustacean parts, copepods, plant material and polychaetes make up the remainder. Some of the organic debris results from trituration of ingested tissues, but an undetermined portion is ingested as detritus.

In the laboratory, shrimp grow rapidly on diets of *Artemia salina, Mercenaria mercenaria* and hard-boiled egg. Fish meal, copepods, beef liver, tropical fish food, agar enriched with glycogen, bacteria, and *Spartina alterniflora* detritus with associated microflora are also utilized, but growth is retarded.

Crangon septemspinosa utilizes a variety of foods. The shrimp have a preference for animal tissues of marine origin and grow best on these foods, but they have the ability to utilize food of microbial and terrestrial origins.

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